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Occurrence of "*Hippotherium*" in the Old World: a revision of two hipparion species in Eurasia

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Abstract A controversial taxon, *Hipparion plocodus*, is reviewed in the present study. *Hi. plocodus* has been confirmed to be a valid species with definite diagnostic characteristics, represented by cranial specimens from Baode, Shanxi Province. The phylogenetic analysis performed in the present study, with a new matrix, shows that *Hi. plocodus* forms a monophyletic group with a European species, *Hippotherium malpassii*. Actually, no close relationship between so-called *Hm. malpassii* and the genus *Hippotherium* has been identified, and the record of stratigraphic range of this genus in late stage of Late Miocene is currently absent. Herein previously *Hi. plocodus* and *Hm. malpassii* have both attributed into "*Hipparion*" before the discovery of better material. Evolutionary stages and correlative absolute age showed that these two species should derive independently from some primitive clade. During the late stage of the Late Miocene, the development of the Asian summer monsoon enhanced the humidity of China, with forest and wood habitats expanding considerably under this setting. As the result, one Eurasian closed-habitat lineage thus extended its range into China, which had become very suited for it, give rise to "*Hi.*" *plocodus*.

Key words systematic revision, phylogeny, Eurasian hipparion, paleozoogeography

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1 Introduction

Hippotherium primigenium has been traditionally considered to be the earliest and the most primitive hipparion species in Eurasia. It was considered the best representative for the significant biozoogeographic event, the *Hippotherium* Datum, which was the first occurrence of *Hippotherium* in the Old World during the Late Miocene (Bernor et al., 1987; Alberdi, 1989; Sen, 1989; Garcés et al., 1997). Hitherto classification of the hipparion horse

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has been controversial. Some authors have placed the *Hm. primigenium* into the generic group *Hippotherium* (Bernor et al., 1997; Zouhri and Bensalmia, 2005; Woodburne, 2005, 2007). Others argue that all hipparion species in the Old World should be assigned within one genus, *Hipparion* and that the taxon *Hippotherium* should be regarded as a subgenus (Bernor et al., 1997; Zouhri and Bensalmia, 2005; Woodburne, 2005, 2007). Some species of genus/subgenus *Hippotherium* have also been placed in other groups ("*Cormohipparion*" *africanum* [=*Hipparion* (*Hippotherium*) *africanum*], Bernor and White, 2009; *Cormohipparion* [=*Hipparion* (*Hippotherium*) *primigenium*], Bernor et al., 2018). Woodburne and Bernor (1980) defined superspecific/infrageneric units for the genus *Hipparion* in the Old World. They divided the genus into four groups, mainly based on facial morphology. The four-group framework was applied for a decade (Bernor, 1985; MacFadden and Woodburne, 1982; Bernor and Hussain, 1985; Bernor et al., 1987, 1990). Among them, the Group 1 consists of all the primitive forms from the Vallesian period, and some Turolian period ones. Bernor et al. (1996) proposed the concept of the *Hippotherium primigenium* complex, which is equivalent to the former Group 1. This complex consists of the definite member *Hm. primigenium* and other potential relative forms, such as "*Hm.*" *koenigswaldi*, "*Hm.*" *catalaunicum*, "*Hm.*" *sitifense*, "*Hm.*" *depereti*, "*Hm.*" *brachypus*, and "*Hm.*" *giganteum*. Qiu et al. (1987) argued that subgenus *Hippotherium* was equivalent to Group 1 of Woodburne and Bernor (1980). They ascribed all the Bahean forms in China and European forms, such as *Hm. africanum*, and *Hm. catalaunicum*, to this subgenus. In the present study, we adopt the classification framework to treat *Hippotherium* as a generic unit.

The most recent chronological data notes that the oldest record of European hipparion was at 11.4–11.0 Ma from the Pannonian C locality, Vienna Basin, which was the first identified as *Hippotherium* sp. (Bernor et al., 2017). Bernor et al. (2018) argued that the hipparion forms that occurred in Eurasia and Africa between 11.4 and 11.0 Ma should be assigned to the genus *Cormohipparion*, while even the concept of the *Hippotherium* Datum should be changed to the *Cormohipparion* Datum. Based on the figures in Bernor et al. (2017), however, we tend to ascribe the Pannonian specimens as *Hm. primigenium*. Bernor et al. (1999) reported hipparion specimens from the Pannonian Basin in Hungary and identified them as *Hippotherium sumegense* and "*Hipparion*" sp. small. They indicated that *Hm. sumegense* occurred in the late Vallesian, i.e., MN (Mammal Neogene) 10, ca. 9.5 to 9.0 Ma. Kaiser et al. (2003) reported hipparion species from Rheinhessen, Germany, and identified them as *Hm. kammerschmitti*. They assigned diagnostic characteristics for this species, including them being slightly smaller than *Hm. primigenium*, the Mc III being moderately long, and the cheek teeth being slightly narrower and shorter, but morphologically identical to *Hm. primigenium*. They indicated that the age of *Hm. kammerschmitti* was early Turolian age, i.e., MN11. Bernor et al. (2003) reported hipparion specimens from Rudabánya,

Hungary, and identified some of them as *Hm. intrans*. They argued that this species was valid and represented an advanced member of the *Hm. primigenium*. They indicated that the age of the fauna in Rudabánya was from MN 9. The earliest record of Asian hipparion forms is represented by *Hi. dongxiangense* and *Hm. weihoense*, the first occurrence of which were both around 11.5 Ma in Guonigou and Bantu localities, the Linxia Basin (Deng et al., 2013; Fang et al., 2016; Sun et al., 2022). The classical Bahean (early stage of Late Miocene) localities in China, including Lantian and Fugu, Shaanxi Province, both yield specimens of *Hippotherium*. The Damiaogou locality in Lantian area is the type locality for the most widespread species of genus *Hippotherium*, *Hm. weihoense*, and *Hm. chiai*. The magnetostratigraphic data in Lantian area (Zhang et al., 2013) showed that the first and last occurrences of *Hm. weihoense* were at 8.21 and 7.91 Ma, respectively, while those of *Hm. chiai* were at 8.21 and 7.26 Ma, respectively. The record of *Hm. chiai* in Fugu occurred within the Lamagou fauna, with an age of 7.8 Ma (Xue et al., 2006; Li et al., 2023). Biostratigraphic data of Deng et al. (2013) shows that the last occurrences of *Hm. weihoense* and *Hm. chiai* in Linxia Basin were both not later than 8.7 Ma.

Under the Chinese stratigraphic timescale framework, the Late Miocene is divided into two stages, the Bahean (early) and Baodean (late), with a boundary at 7.25 Ma. As discussed above, no species of *Hippotherium* in the Old World survived into the Baodean. However, Bernor et al. (2011) identified a new species, *Hm. malpassii*, based on specimens from the Baccinello V3 area in Italy, with an age of around 6.7 Ma based on their magnetostratigraphic data. Rook and Bernor (2013) reported additional specimens of this species from the Monticino gypsum quarry in Brisighella, Emilia-Romagna, Italy, with an estimated age of MN13. They argued that the Monticino specimens represented the youngest known record for *Hippotherium* in Eurasia. In China, a Baodean hipparion species, *Hipparion plocodus*, is very similar to *Hm. malpassii* in terms of dentition morphology. In contrast with *Hm. malpassii*, which lacks adequate cranial morphology information from an adult individual, several well-preserved skull specimens of *Hi. plocodus* have been found among the Frick Collection housed in AMNH. The combination of known specimens of *Hi. plocodus* and *Hm. malpassii* helps to resolve the puzzle of whether *Hippotherium* survived until 7.25 Ma, i.e., the Bahean/Baodean boundary. The research on these two species will also improve our understanding of *Hippotherium* and the boundary between the Bahean/Baodean stages, the significant node for the evolution of Eurasian hipparion.

Abbreviations AMNH, American Museum of Natural History; F:AM, specimen number of the Frick Collection of AMNH; IGF, Museo di Storia Naturale (Sezione Geologia e Paleontologia) of the University of Florence; NHMB, Basel Naturhistorisches Museum; PMU, Palaeontology collections, Museum of Evolution, Uppsala University, Uppsala, Sweden. Avg, average value; FI, length index of postflexid, ratio between lengths of postflexid and

tooth, then the value multiply by 100; FL, length of postflexid; IOF, infraorbital foramen; L, length; Max, maximum value; Mc III, the third metacarpal; Min, minimum value; Mt III, the third metatarsal; N, Number of samples; PL, length of protocone; POB, preorbital bar; POF, preorbital fossa; PW, width of protocone; W, width.

2 Geological background

The AMNH and PMU specimens were collected from Andersson Lok. 49 (Yangmugou), Baode, Shanxi, China (N 39°00′, E 111°10′, H 1024 m). All the specimens were collected from tunnels in this locality. In a recent field work, two tunnels can be seen in Yangmugou. A thick layer of gravel overlies the entrances of the tunnels, while their walls consist of red-brown clay or clayey silt, coarsening up to yellowish-brown silt and capped by laterally continuous calcrete horizon. The species found in Lok. 49 include Amphicyon indet. (or probably a milk tooth of an elephant), *Proputorius minimus*, *Plesiogulo brachygnathus*, *Lutra aonychoides*, *Melodon majori*, ?*Melodon incertum*, *Promephitis* cf. *P. maeotica*, *Hyaenictitherium wongii*, *H. hyaenoides*, *Ictitherium viverrinum*, *Adcrocuta eximia*, ?L*ycyaena dubia*, *Machairodus palanderi*, *Metailurus parvulus*, *Felis* sp., "*Mammut borsoni*", "*Mammut* sp.", "*Hi.*" *plocodus*, *Dihoplus ringstroemi*, *Chilotherium* sp., *Acerorhinus paleosinense*, *Chleuastochoerus stehlini*, *Propotamochoerus hyotherioides*, Suidae gen. et sp. indet., *Cervavitus novorossiae*, *Procapreolus latifrons*, Cervidae gen. et sp. indet., *Palaeotragus microdon*, *Palaeotragus* sp., *Honanotherium schlosseri*, *Urmiatherium intermedium*, *Gazella gaudryi*, *Gazella* sp. aff. *gaudryi*, *G.* ?*paotehensis*, *G. dorcadoides*, *Gazella* sp., ?*Dorcadoryx lagrelii*, P*alaeoryx sinensis*, and Bovidae gen. et sp. indet. (Tong, 2012; Kaakinen et al. 2013; present study).

3 Materials and methods

3.1 Materials, terminology, and measurements

The material described in the present work is housed in PMU, and AMNH. The terminology of maxilla and mandible structures follows Sisson (1953); that of dentition follows Qiu et al. (1987). All measurements follow Eisenmann et al. (1988), and were taken using calipers to the nearest 0.1 mm (Tables 1–3).

3.2 Phylogenetic analyses

On the basis of work of predecessors, we created a new data matrix. The phylogenetic analysis was performed using TNT 1.1 with a traditional research method (Goloboff et al., 2008); 1000 replications and the trees–bisection–reconnection branch–swapping algorithm (TBR) were applied in our analyses. All characters are equally weighted and non–additive. Gaps are treated as "missing", and multistate taxa are interpreted as polymorphism.

Table 1 Skull measurements of "*Hipparion*" *plocodus* (mm)

item	M 3824	M 3825	AM 146439	AM 146440	AM 146441	AM 146442	AM 146443	AM 146448
muzzle length	117.2	107.9	114.1	109.5		108		109
palatal length	101.3	104.4	99.3	99.2	103.5	103.8	104.1	96
vomerine length								92.2
premolar length	74.7	75.7	67.6	73.1	67.9	73.8	71.4	63.8
molar length	59.5	59	52.9	57.7	56.8	60.9	57.9	54.5
upper cheek teeth length	136	137	120.3	128.7	125.5	134.9	130.3	118.3
minimal breadth of choanae				33.7	34.1		30.3	31
maximal breadth of choanae				36.3	41	39	35.5	37.2
palatal breadth	66.6	64.9	58.3	59.3	59.4	63.2	57	53.1
minimal muzzle breadth	35.5	35.3	35.5	35.9		37.1		35.7
muzzle breadth	42	46.9		52.5		55.4	51.6	48.6
frontal breadth							140.5	
anterior ocular line								311.8
facial height								83.7
antero-posterior orbital diameter								53.4
orbital diameter perpendicular to the former								50.2
length of the naso-incisival notch				113.3				109
cheek length				150.5			149.7	151.6
POB length			37.2	32.1	40.9		37	30.8
POF length			90.3	81.5			87.2	87.3
distance between the back of POF and IOF				60.6			57.9	60.6
height of the POF			42.4	43.5			43	52.3
distance between POF and the facial crest			24.3	41.3	36.2		40	27.6
height of back of IOF				47.9			43.1	45.6
height of the back of POF above the alveolar border			72.3	75.6	69.4		82.5	77.2

Table 2 Upper cheek tooth measurements of "*Hipparion*" *plocodus* (mm)

Teeth	N	Measures	Avg	Min	Max
P2	4	L	27.4	24.9	28.6
	2	W	20.8	19	22.5
	3	PL	6.7	5.6	8.4
	2	PW	3.7	3.4	4
P3	6	L	21.3	18.6	22.6
	5	W	21.6	20.6	23
	6	PL	6.3	4.9	8
	5	PW	4.1	3.1	5.2
P4	6	L	20.0	18.7	21.3
	5	W	21.0	20.2	22.4
	6	PL	6.0	4.8	7
	6	PW	4.4	3.3	5.7
M1	6	L	17.7	16.2	19.2
	5	W	19.4	18.9	20.1
	6	PL	6.1	4.6	6.7
	6	PW	4.0	2.7	5.1
M2	6	L	18.0	16.4	19.1
	4	W	19.0	18.3	19.8
	6	PL	5.7	4.7	6.4
	5	PW	4.1	3	4.8
M3	6	L	20.4	19.1	22.9
	5	W	18.4	15.7	24
	6	PL	5.6	5.1	6
	5	PW	3.6	2.5	4.9

Table 3 Lower cheek tooth measurements of AMNH F:AM 146708 (mm)

Tooth	item	Measurement	Tooth	item	Measurement
P2	L	26.6	M1	L	19.8
	W	12.7		W	11.7
	FL	11.2		FL	8.1
	FI	42.1		FI	40.9
P3	L	22.9	M2	L	20.3
	W	14.7		W	10.8
	FL	10.1		FL	7.2
	FI	44.1		FI	35.5
P4	L	21.2			
	W	14.4			
	FL	8.9			
	FI	42.0			

4 Systematics

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Subfamily Equinae Steinmann and Doderlein, 1890

Tribe Hipparionini Quinn, 1955

Genus "*Hipparion*" (de Christol, 1832)

"*Hipparion*" *plocodus* (Sefve, 1927)

(Fig. 1; Tables 1–3)

"*Hipparion plocodus*" Sefve, 1927; Bernor et al., 1990, p. 52

Type specimens PMU M 3824, lectotype, housed in the Museum of Evolution of Uppsala University, Uppsala, Sweden, assigned by Forstén in 1968.

Type locality and horizon Baode, Shanxi, Late Miocene, Baodean.

Referred specimen PMU M 3825, broken maxillary with snout and dentition series; AMNH F:AM 146439-146442, four fragmental skulls; AMNH F:AM 146443, middle part of skull and snout part of one individual; AMNH F:AM 146448, a relatively complete skull of an old individual; AMNH F:AM 146708, left ramus of mandible with p2–m2. All collected from Baode, Shanxi.

Revised diagnosis Small-sized hipparion horse. Moderately robust muzzle. Nasal notch usually very anterior to P2. POB short (<40 mm). POF strong, elongated with distinct anterior margin. Cement on cheek tooth thick. Anterostyle/anterostylid short. Plications in pre– and postfossettes strong and complex at middle wear stage. Pli caballine usually single to double, sometimes complex. Protocone usually very rounded. Hypoconal groove deep at middle wear stage. Protostylid usually present. Metaconid and metastylid both subtriangular. Pli caballinid usually present on premolar at middle wear stage.

Descriptions Cranium: The muzzle is moderately robust and the bottom of the nasal notch is located at the level in front of the P2. The sphenoid body is narrow and high ventrally. The base of the pterygoid process is anteriorly located at the level in front of the temporal condyle. The pterygoid crest is weak and diverges slightly laterally. The foramen lacerum is large. The central flat part of the dorsal surface of the frontal bone is narrow, and the lateral parts are inclined such that the supraorbital foramen and the upper orbital margin are lower than the frontal surface. The postorbital process is transversely wide, anteriorly concave, posteriorly convex, and relatively thin in lateral view. The free parts of the nasal bones are thin and extend anteriorly, and the posterior parts are long and strongly inclined laterally. The lacrimal sac fossa is rounded and is located at the anterosuperior corner of the orbital surface. The anterior half of the upper orbital margin is a wide and deep notch. The zygomatic process of the zygomatic bone reaches the posterior orbital margin. Its ventral surface is wide, and its lateral side is a rough surface for muscular attachment. The midpoint of the posterior border of the hard palate is located at the level of the anterior margin of the M2 protocone; the anterior palatine foramen is at the level of the M2 hypocone. The pterygoid process of the pterygoid bone is low and erect, with a central groove. The POF is strong and very elongated with a relatively deep posterior pocket and a clear anterior margin, while the POB is short (<40 mm). The facial crest ends above the posterior margin of P4. IOF is located above the P3/P4 boundary near the upper border

of the maxillary bone. The facial surface of the maxillary bone is strongly constricted in front of P2 to form a large and deep buccinator fossa. The nasal process gradually becomes slender posteriorly and disappears above the midline of P2 in lateral view. The I1 cup has thick enamel and fine lingual wrinkles. The lingual surface of I1 has a wide and shallow groove. The I2 cup is elongated and labiolingually constricted, while the I3 cup is subtriangular with thin enamel.

P2: The anterostyle is short. The labial walls of the para- and metacone are flat. The plications in the fossettes are complex, especially the plis protoloph. The protocone is rather rounded. The pli caballine is double to complicated. The hypoconal groove is wide and deep and the hypoconal constriction is weak to absent.

P3: The parastyle is pointed and extends labially. The labial walls of the para- and metacone are concave. The horns of the pre- and postfossette are oblique and rounded at the tips. The protocone is rounded to oval. The plications in the fossettes are similar to P2 except that the plis protoloph is simpler. The pli caballine is usually bifid. The hypoconal groove is wide and deep and the hypoconal constriction is usually present.

P4: Similar to P3 in morphology but longer than P3 in size.

M1/2: Similar to P3 and P4 in morphology, but smaller in size. The plications in the fossettes are more complex than the premolars. The para- and mesostyle are slenderer. The hypoconal groove is narrower and shallower.

M3: Usually the smallest cheek tooth. It is rectangular or triangular, depending on its stage of wearing. The mesostyle is short and narrow. The plications in the fossettes are simple.

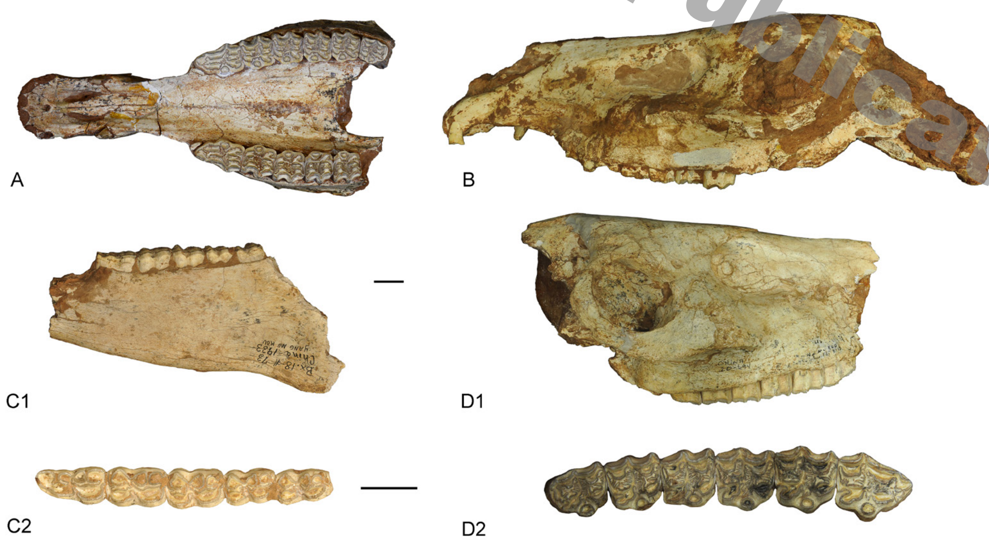

Fig. 1 “*Hipparion*” *plocodus* in Lok. 49, Baode, Shanxi
A. ventral view of lectotype PMU M 3824; B. left view of AMNH F:AM 146448; C. AMNH F:AM 146708: C1. left view, C2. occlusal view of cheek tooth row; D. AMNH F:AM 146443: D1. left view, D2. occlusal view of left cheek tooth row. Scale bars = 2 cm

The hypoconal groove is usually shallow but sometimes may form an isolated circle at later stages of wearing.

p2: The metaconid is small and oval. The metastylid is large, leaf-shaped with a short stem, and extends more lingually. Linguaflexid opens towards the labial side. The linguaflexid is U-shaped. The entoconid is big and irregular. The protoconid is small and oval. The hypoconid is robust with flat lingual and labial walls. The pli caballinid is absent. The ectoflexid is shallow, and far from the isthmus. The postflexid is elongated with a swollen bottom.

p3: The parastylid is small and simple and extends lingually. The metaconid and metastylid are subtriangular. The linguaflexid is wide and U-shaped. The isthmus is slightly oblique anteriorly. The entoconid is smaller while the hypoconulid is very small. The labial wall of the protoconid is flat, and the hypoconid is elongated, with a flat labial wall. The anterior horn of the preflexid is long and extends labially, while the posterior one extends posteriorly. The postflexid is elongated. The ectoflexid reaches the opening of the isthmus with a tip that extends anteriorly.

p4: The p4 is similar to p3 but slightly smaller. The metastylid is slightly shorter, while the pli caballinid is stronger and the ectoflexid is closer to the opening of the isthmus.

m1 is similar to m2, while the main differences between p3 and p4 are that the paraconid extends more lingually and the metaconid and metastylid are obviously subtriangular.

Remarks Forstén (1968) undertook a massive revision of the Chinese species of hipparion, synonymized eight species established or reviewed by Sefve (1927) as the species “*Hipparion*” *plocodus* (her *Hi. plocodus*). Among these species, *Hi. richthofeni* was a mixture of different lineages of hipparion, which had confused researchers for decades. Sefve (1927) classified some specimens from Baode, Shanxi, into this species. Gromova (1952) suggested that although the species *Hi. richthofeni* should be invalid, the specimens Sefve ascribed as this species represent a valid taxon. Zhegallo (1971) defined a new species, *Hi. forstenae*, for these Sefve specimens. Qiu et al. (1987) erected new subgenus *Cremohipparion*, attributed this species of Zhegallo (1971) into this subgenus (which in our opinion should be a genus), and assigned a lectotype for *Cr. forstenae*. Bernor et al. (1990) also accepted the validity of *Cr. forstenae* (their “*Hi.*” *forstenae*) and reassigned a lectotype. *Hipparion fossatum* and *Hi. coelophyes* were considered as synonyms by Qiu et al. (1987), where they accepted the validity of *Hi. fossatum* due to priority on pagination. In a footnote, however, they explained that they intended to abolish the species *Hi. fossatum* based on a wrong assignment of lectotype for *Hi. fossatum* by Forstén (1985). Later authors also accepted the validity of *Hi. coelophyes* (Bernor et al., 1990; Pang, 2015). Qiu et al. (1987) considered *Hi. kreugeri* as a synonym of *Cr. hippidiodus* (their *Hi. hippidiodus*). *Hipparion parvum* was treated as a nomen dubium by Qiu et al. (1987) and Bernor et al. (1990) due to its rare material. Qiu et al. (1987) condisered

that *Sivalhippus ptychodus* (their *Hi. ptychodus*) and *Hi. tylodus* were both synonyms of *Si. platyodus* (their *Hi. platyodus*). Bernor et al. (1990) argued that *Hi. tylodus* should be treated as a nomen dubium, but *Si. ptychodus* (their "*Hi.*" *ptychodus*) was a valid species based on its facial morphology and was different from *Si. platyodus.* Sun et al. (2018) performed a morphological comparison on both the facial part and dentition and quantity analyses, and accepted the validity of *Si. ptychodus.*

As discussed above, all the species listed as synonyms for "*Hi.*" *plocodus* by Forstén (1968) should represent other valid species. Consequently, the diagnosis that Forstén (1968) had assigned for "*Hi.*" *plocodus* was actually a mixture from multiple taxa. Bernor et al. (1990) treated "*Hi.*" *plocodus* (their "*Hi. plocodus*") as a nomen dubium. Previously, Qiu et al. (1987) had argued for the validity of "*Hi.*" *plocodus* (their *Hi. plocodus*). Qiu et al. (1987) described a skull from the Frick Collection and indicated that the dentition features of this skull are identical to those of Sefve (1927)'s specimens, based on which they defined the species "*Hi.*" *plocodus* (their *Hi. plocodus*). In addition, the Frick skull and Sefve's specimens were all collected from Andersson locality 49 in Baode, Shanxi. Qiu et al. (1987) argued that this skull should be attributed to "*Hi.*" *plocodus* (their *Hi. plocodus*) and suggested that the cranial morphology consisted of massive POF, short POB (<40 mm), and a very shallow nasal notch. Unfortunately, most Chinese specimens in the Frick Collection had not been formally cataloged, e.g., Qiu et al. (1987) did not note the specimen number nor provide a picture of this skull. The first author of this manuscript found a skull during a visit to the AMNH in 2017, which is probably the skull of "*Hi.*" *plocodus* described by Qiu et al. (1987), as the cranial and dentition features perfectly fit their description. In addition, a complete skull belongs to an aged individual, and other partial cranial specimens were also found in Frick Collection, which had been collected from the same locality, Andersson locality 49, with similar morphological characteristics. In comparison with specimens in the Lagrelius Collection, which Sefve based the species "*Hi.*" *plocodus* (his *Hi. plocodus*), the Frick specimens are identical to the Lagrelius specimens with respect to dentition features, fitting the description of Qiu et al. (1987). The series of skulls in the Frick Collection, therefore, shows a distinct combination of cranial characteristics. Hence, "*Hi.*" *plocodus* should be regarded as a valid species.

5 Discussion

5.1 Morphological comparison

Qiu et al. (1987) proposed a potential relationship between *Sivalhippus platyodus* and "*Hipparion*" *plocodus*. In their diagnostic characteristics list, *Si. platyodus* had a large variation range of cheek tooth row lengths, from 125 mm to 150 mm, which is rare for

intraspecific variation in hipparion species. "*Hi.*" *plocodus* is a small-sized form of hipparion (Tables 1, 3), with *Si. platyodus* being larger. The lectotype skull of *Si. platyodus* has a cheek tooth row with a length of more than 140 mm. A recently collected skull of *Si. platyodus* from the Duikang locality in Linxia Basin, Gansu, has cheek tooth rows with lengths of around 150 mm. Although "*Hi.*" *plocodus* shares some dentition features with *Si. platyodus*, such as very complicated fossette ornamentation and pli cabalinine, some differences are still present: The pli caballinids of "*Hi.*" *plocodus* are very weak to absent, in contrast to the usually clear to strong pli caballinids of *Si. platyodus*. *Hi. coelophyes* is another species with close morphological features to "*Hi.*" *plocodus*. These two species share some characteristics, including small body size, shallow nasal notch, complicated fossette ornamentation, subtriangular metaconid-metastylid complex, and short metapodial, with *Hi. coelophyes* having obvious differences from "*Hi.*" *plocodus* in terms of cranial and dentition morphology. *Hi. coelophyes* has a long POB (>40 mm), oval protocone rounded lingually, and flat labially, with its posterior margin of the nasal notch at the level above the anterior margin of P2, obviously deeper than that of "*Hi.*" *plocodus*. In addition, an interspecific variation seems to be present in the POF of *Hi. coelophyes*. The lectotype skull of this species assigned by Bernor et al. (1990), collected from Baode, has a clear but shallow POF. In contrast, the skull reported by Pang (2015), collected from the Shilei locality in the Linxia Basin, Gansu, has a strong and deep POF.

All of the species assigned to *Plesiohipparion* and *Proboscidipparion* are large, advanced forms, with basilar and cheek tooth row lengths no less than 430 mm and 140 mm, respectively. The basilar length of the lectotype of *Pr. sinense* is even up to 500 mm. *Plesiohipparion* and *Proboscidipparion* share some features with "*Hi.*" *plocodus*, such as complicated fossette ornamentation and pli cabalinine. However, "*Hi.*" *plocodus* has some features distinct from the other two, including very rounded protocone, not a strongly triangular metaconid-metastylid complex, and deep ectoflexids on the premolars and molars. *Si. theobaldi* is another species in *Sivalhippus* in addition to *Si. platyodus*. Differently from *Si. platyodus*, *Si. theobaldi* is a very large hipparion form, although *Si. theobaldi* shares most dentition characteristics with *Si. platyodus.* However, considering some specimens from Lufeng, Yunan Province, China, and some from the Siwalik Hills, India, *Si. theobaldi* usually has a more rounded protocone than *Si. platyodus.*

Baryhipparion is one of the largest hipparion forms in terms of size, represented by *B. insperatum* found in localities in North China. Except for the very large size, however, *B. insperatum* is identical to "*Hi.*" *plocodus* in terms of cranial morphology. *B. insperatum* has a shallow nasal notch and very elongated and strong POF. Based on the holotype skull of *B. insperatum*, this species should have a short POB (<40 mm). All of these fit the diagnostic characteristics of "*Hi.*" *plocodus*. On the other hand, *B. insperatum* also shows clear

differences from "*Hi.*" *plocodus* in morphology, with simple but fine fossette ornamentation and pli cabaline, and rounded protocone. The marked feature of *B. insperatum* is the combination of lower dentition characteristics consisting of a rounded metaconid-metastylid complex and very deep ectoflexid, even on the premolar.

Shanxihippus dermatorhinum is a very large hipparion from China, with basilar and cheek tooth row lengths around 450 mm and 150 mm, respectively. *Sh. dermatorhinum* was considered to be close to *Cremohipparion* and *Proboscidipparion* (Qiu et al., 1987). Deng (2012) considered this species to be a potential relative of *Pr. sinense.* These conclusions were based on the very elongated snout and retracted nasal notch. Phylogenetic analysis by Bernor et al. (2018) suggested that *Sh. dermatorhinum* formed sister groups with *Proboscidipparion*. They erected a new genus, *Shanxihipparion*, for species *Hi. dermatorhinum* based on its specialized characteristic complex. *Sh. dermatorhinum* shares some dentition characteristics with "*Hi.*" *plocodus*, but to a lesser degree, with uncomplicated fossette ornamentation, nor such a strong angle on the metaconid-metastylid complex as the latter. *Sh. dermatorhinum* also has a more elongated protocone than that of "*Hi.*" *plocodus*. *Hi. brachypus* is a species only found in Europe, with a body size similar to that of *Sh. dermatorhinum*. These two species share some characteristics with regards to cranial and dentition morphology, however, *Hi. brachypus* also shows some clearly more primitive features than *Sh. dermatorhinum*, as represented by a shallower nasal notch.

Cremohipparion was defined by Qiu et al. (1987) for a series of species that share similar characteristics, such as a free portion of nasal with a ventrally projected and incurved lateral rim, short POB (<40 mm), conspicuous POF, and subnasal fossa. The species in this subgenus also share similar dentition characteristics, such as simple fossette ornamentation and pli cabaline, and rounded protocone and metaconid-metastylid complex. Although most characteristics of *Cremohipparion* are distinct from those of "*Hi.*" *plocodus*, they share some facial features such as short POB (<40 mm) and strong and very elongated POF, especially present in the advanced form in *Cremohipparion*, such as *Cr. licenti*, which occurred in the Pliocene. The status of *Cr. hippidiodus* was previously unclear (*Hi. hippidiodus*, Qiu et al., 1987; "*Hi.*" *hippidiodus*, Bernor et al., 1990). Liu (2013) firstly proposed that this species should attributed into genus *Cremohipparion*. The skull collected from the Shilei locality in the Linxia Basin was identified by Pang (2015) as *Cr. hippidiodus* (her *Hipparion hippidiodus*), which is the most complete known skull of this species. The Shilei skull shows a series of features similar to other forms in *Cremohipparion*, including a ventrally projected lateral rim of the nasal, and a weak but present subnasal fossa. *Cr. hippidiodus* is primitive in morphologic characteristics, and it could be considered a potential ancestral type for *Cremohipparion*.

By morphological comparison, the closest hipparion form to "*Hi.*" *plocodus* is "*Hi.*" *malpassii* found in Italy. Based on the diagnostic characteristics list of Bernor et al. (2011), "*Hi.*" *malpassii* is a moderately-sized species with a long preorbital bar, preorbital fossa with moderate medial depth, and slightly pocketed posterior margin. The upper cheek tooth is extremely richly plicated and the pli caballin is richly and complexly ornamented (Fig. 2). The protocone varies from oval to small rounded, the lower cheek tooth has a substantially larger metaconid than metastylid. Oval protocones account for a certain ratio in "*Hi.*" *malpassii*, but most dentition specimens of "*Hi.*" *plocodus* have very rounded protocones (Fig. 2, Table 2). The metaconid-metastylid complex of "*Hi.*" *malpassii* shows a trend to be subtriangular, but still more rounded than that of "*Hi.*" *plocodus*. "*Hi.*" *malpassii* is actually the species closest to "*Hi.*" *plocodus* in terms of size, as well as cranial and dentition morphology. The results of the phylogenetic analysis also support the notion that these two species form a monophyletic clade.

Fig. 2 Comparison on occlusal morphology of upper cheek teeth of "*Hipparion*" *plocodus* and "*Hi.*" *malpassii*
A. left cheek tooth row of lectotype of "*Hi.*" *plocodus*, PMU M 3824; B. left cheek tooth row of "*Hi.*" *plocodus*, AMNH F:AM 146443; C. left cheek tooth row of holotype of "*Hi.*" *malpassii*, IGF 9400V (Bernor et al., 2011:fig. 13b); D. left P2 of "*Hi.*" *malpassii*, NHMB JH 126A (Bernor et al., 2011:fig. 15b); E. left P3 of "*Hi.*" *malpassii*, NHMB JH 126B (Bernor et al., 2011:fig. 15c); F. left M1 of "*Hi.*" *malpassii*, NHMB JH 126D (Bernor et al., 2011:fig. 15e); G. right P4 of "*Hi.*" *malpassii*, NHMB JH 126F (Bernor et al., 2011:fig. 15f). Scale bar = 4 cm

5.2 Phylogeny

Qiu et al. (1987) have reviewed species of hipparion horse in China, and assigned 18 valid species, attributing them to seven subgenera. They also summarized and illustrated the phylogenetic relationship between Chinese species and some important forms in Europe and Africa. In their taxonomic framework, the subgenus *Hipparion* was considered as a polyphyletic group, which consisted of *Cremohipparion hippidiodus* (their *Hi. hippidiodus*), *Shanxihippus dermatorhinum* (their *Hi. dermatorhinum*), *Si. platyodus* (their *Hi. platyodus*), "*Hi.*" *plocodus* (their *Hi. plocodus*), *Hi. coelophyes*, and *Hi. mongolicum*. They considered "*Hi.*" *plocodus* to likely be in the same clade as *Si. platyodus*, the latter likely to have given rise to genus (their subgenus) *Plesiohipparion*, while the detailed evolutionary history of "*Hi.*" *plocodus* was not clear. In the framework of Qiu et al. (1987), the last occurrence of *Hippotherium* was at the Bahean/Baodean boundary, with all Baodean specimens of hipprion in China respectively originating from several unknown lineages rather than the subgenus *Hippotherium*. Sun and Deng (2019) performed a new review of Chinese species of *Hipparion*. Although they followed the main part of the framework of Qiu et al. (1987), with respect to the origin of Chinese hipparion, they argued that most species of Chinese hipparion were derived from *Hippotherium*. They also proposed that "*Hi.*" *plocodus* had a close relationship to *Hi. coelophyes*. The most recent phylogenetic analysis on Chinese hipparion species was performed by Bernor et al. (2018), in which some species were selected from *Cremohipparion*, *Sivalhippus*, *Shanxihipparion*, and *Proboscidipparion*, and formed a clade, which was composed of sister groups with *Hippotherium weihoense*. Some discussions about the phylogenetic relationships of Chinese hipparion have been published recently (Deng et al., 2016; Bernor et al., 2018; Sun et al., 2018), but more comprehensive analyses still need to be performed.

We used the characteristic list from Woodburne (2007) as our basis and revised and added some more cranial, dentition, and postcranial features. We use *Parahippus leonensis* and *Merychippus primus* as the outgroup taxon. We selected the North American species *Cormohipparion goorisi*, *Co. quinni*, and *Co. occidentale*, the European species *Hm. primigenium*, *Hm. Catalaunicum*, *Hipparion brachypus* and "*Hi.*" *malpassii*, the North African species *Hm. africanum*, the Chinese species *Hm. weihoense*, *Cremohipparion forstenae*, *Cr. hippidiodus* and *Cr. licenti*, *Baryhipparion insperatum*, *Si. platyodus* and *Si. theobaldi*, *Plesiohipparion huangheense* and *Pl. houfenense*, *Proboscidipparion pater* and *Pr. sinense*, "*Hi.*" *plocodus*, and *Shanxihippus dermatorhinum*. We obtain a new matrix with 23 taxa and 63 characteristics (see Supplemental Information 1, 2). Two MPTs (most parsimonious tree) are obtained via analysis, the consensus tree is present in Fig. 3.

Based on the results of the phylogenetic analysis, except for the genus species in *Cormohipparion*, namely *Hm. weihoense*, *Hm. catalaunicum*, and *Hm. africanum*, the other

taxa form a monophyletic group, which forms sister groups with *Hm. africanum*, the most advanced species in *Hippotherium*. This result suggests that *Hippotherium* has a basal position within Old World hipparion lineage. Nevertheless, the species in this genus form a paraphyletic group.

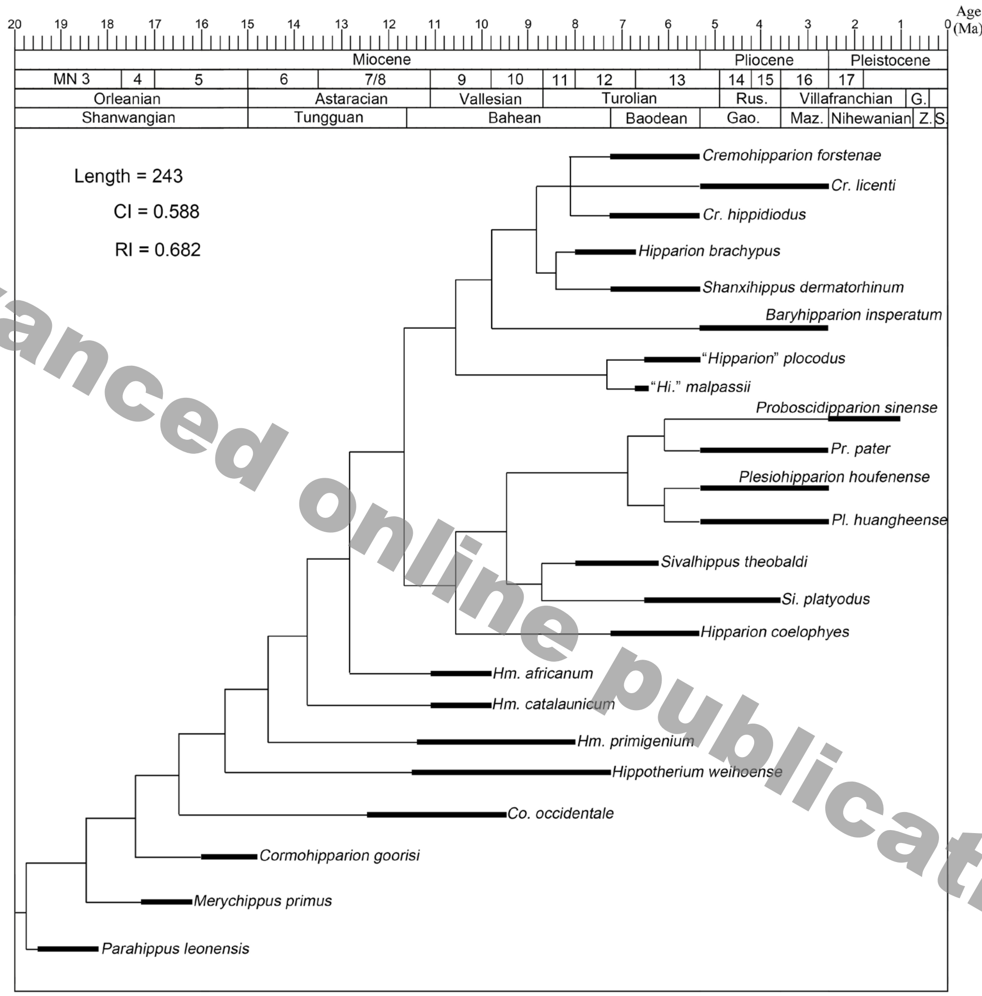

Fig. 3 Correlation of geographical distributions and phylogenetic relationship of *Cormohipparion* and Eurasian hipparion lineage based on the strict consensus tree from most–parsimonious trees
Abbreviations: CI. consistency indece; G. Galerian; Gao. Gaozhuangian; Maz. Mazegouan; MN. Mammal Neogene zones; RI. consistency indece; Rus. Ruscinian; S. Salawusuan; Z. Zhoukoudianian

Hippotherium primigenium was usually considered to be the most primitive hipparion species in the Old World. Phylogenetic analysis performed by Woodburne (2007) indicated that *Hm. primigenium* was in the basal position among all the hipparion species in the Old World and should represent the *Hippotherium* Datum. Based on the phylogenetic analyses presented in the present study, however, *Hm. weihoense* was the basal lineage of hipparion in

the Old World. Among species within *Hippotherium*, *Hm. africanum*, and *Hm. catalaunicum* were the most derived forms. They both have very large body sizes and elongated snouts. *Hm. africanum* has the deepest nasal notch among the species in *Hippotherium*, with a posterior margin at the level beyond the anterstyle of P2. *Hm. catalaunicum* has a significantly elongated POF, which was also a derived characteristic usually present in advanced hipparion forms.

A clade occurred and formed sister groups with *Hm. africanum*, which consists of derived forms of Old World hipparion. This clade is further divided into two massive groups, one of which consists of *Baryhipparion*, *Cremohipparion*, *Shanxihippus*, the species *Hi. brachypus*, and the clade consists of "*Hi.*" *plocodus* and "*Hi.*" *malpassii*. In our phylogenetic analysis results, *Sh. dermatorhinum* and *Hi. brachypus* form sister groups. Indeed, these two species share many similar cranial and dentition characteristics (see comparison part). Although phylogenetic relationships are not confirmed, species of *Cremohipparion* are still gathered into one group (see comparison part). This clade forms sister groups with another one consisting of *Sh. dermatorhinum* and *Hi. brachypus*, where they share derived features in nasal apparati, mainly including the highly retracted nasal notch. The forms with specialized nasal apparati were combined as a clade, which forms sister groups with *Baryhipparion*. All of these taxa share some features, such as clear, moderately to extremely elongated POF, deep ectoflexid in the premolar, and relatively low height of the cheek tooth crown. This highly diversified clade, including *Baryhipparion*, *Shanxihippus* and *Cremohipparion* and *Hi. brachypus*, form sister groups with the clade consists of "*Hi.*" *plocodus* and "*Hi.*" *malpassii*. All of these taxa form one of the main clades within the derived forms of Eurasian hipparion. The evolutionary trends in this clade are clear, including body size increase, and POF development and retraction. Some primitive features, such as deep ectoflexid and low height of cheek tooth crown remain and still exist in very late species, such as *B. insperatum* and *Cr. licenti.*

5.3 Biostratigraphy

The Baode area is a classic and standard locality of Late Miocene mammalian fauna in China. Authors have focused on some richly fossiliferous localities in this area, such as localities 30, 44, 49, and 108 (see below). Field surveys, biostratigraphic comparisons, and magnetostratigraphic analyses have been performed, however, the relative and absolute dates of the chronology are still debated.

Zhang et al. (1995) argued that the age of localities 49 and 44 is 5.3 Ma and that of localities 30 and 31 is about 7.4 Ma based on the correlation of mammalian assemblages between Baode and Fugu, Shaanxi. Based on magnetostratigraphic data obtained from the Jijiagou section in Baode, Deng et al. (2004) suggested that the age of locality 49 is about 5.5 Ma and that of locality 30 is between 6.5 and 7 Ma. Xue et al. (2006) estimated the age

of localities 49 and 44 to be about 5.7 Ma and that of localities 30 and 31 about 7.8 Ma. Zhu et al. (2008) argued that Zdansky (1923)'s map shows that locality 49 is at the base, but locality 30 is near the top of the whole deposit, and their survey had confirmed these relative positions.

Kaakinen et al. (2013) performed a barometric survey and accompanying magnetostratigraphic analysis, and showed that in the Baode fossiliferous localities, the oldest ones are localities 31, 43, 44 (lower part), 49, and JJG (Jijiagou) -02, the youngest one is locality 30, and the intermediate aged ones are localities 44 (upper part), 108, and YJG (Yangjiagou) -03. The magnetostratigraphic data showed that the age of locality 30 was around 5.7 Ma, while localities 108 and 49 were 6.5 Ma and 7.0 Ma, respectively. In a comprehensive revision of hipparion assemblages in China, Sun (2024) agreed the magnetostratigraphic data about localities of Baode area of Kaakinen et al. (2013), i.e. the age of locality 49 was around 7.0 Ma.

Rook et al. (2011) performed a magnetostratigraphic analysis on the section that yielded the Baccinello V3 fauna, which consists of "*Hi.*" *malpassii*. The results showed that the fauna correlated to Chron C3An, ca. 6.733 to 6.436 Ma, i.e., MN13. The Monticino specimens of "*Hi.*" *malpassii* were also estimated to be of MN13 age (Rook and Bernor, 2013). "*Hi.*" *plocodus* were at a younger level in the evolutionary stage than "*Hi.*" *malpassii*, based on the discussion above, while the ages of these two species can be considered to be correlative. It seems that these two species had no ancestor-descendant relationship, it is more reasonable to be considered that they were two independent clades from one origin.

5.4 Paleozoogeographic significance

Bernor et al. (2011) hypothesized two extension events of hipparion in Europe. They proposed that some forms of *Hippotherium* originated during the Vallesian age in Central Europe, including Germany and the Pannonian Basin in Austria and Hungary. Later, they dispersed into Greece and Turkey during MN11/12 (ca. 8 Ma). They argued that the occurrence of *Hi. brachypus* was the result of this expansion. In addition, *Hi. brachypus* s.s from Pikermi, Greece, was another form they identified as *Hi.* "*brachypus*", which was distributed in Akkasdagi, Turkey and Samos, Pikermi, Greece, and was also considered to have originated during this expansion. They attributed Pikermi *Hi. brachypus*, Samos, and Akkasdagi *Hi.* "*brachypus*" into their *Hippotherium* clade. The second expansion of forms in *Hippotherium* was represented by the range of their *Hippotherium malpassii* into central Italy during MN13 (around 6.7 Ma).

Based on the phylogenetic analysis results in the present study, however, it is not appropriate to attribute *Hi. brachypus* or "*Hi.*" *malpassii* to the so-called "*Hippotherium* clade". No doubt a dispersion of Eurasian hipparion has been initiated during the early

Turolian. The lineage, which forms sister groups with the most advanced species of *Hippotherium*, *Hm. africanum*, considerably diversified into an enormous group with many monophyletic clades. Either *Hi. brachypus* or "*Hi.*" *malpassii* was a member of these clades. It is difficult to demonstrate the relationship between these two species and the "*Hippotherium* clade" in a brief discussion. In other words, the phylogenetic progress of Eurasian hipparion was more complicated than what we recognized previously. Based on known material and analysis results, Sun et al. (2022) has proposed that *Hippotherium* dispersed throughout Eurasia during the occurrence of *Hippotherium* Datum. In no time, however, Bernor et al. (2022) argued that the data could not supporting the *Hippotherium* Datum in the Linxia Basin and the oldest record of hipparions in the Old World should be *Hippotherium* sp. from the Pannonian C, Vienna Basin. The definition of the first occurrence event of hipparions thus remains a controversial issue. Sun (2024) suggested to use the term "*Hipparion* Datum". During this biotic event, the genus *Hippotherium* underwent adaptive radiation in the Old World (Fig. 4A).

Bernor et al. (2011) sampled an isolated P3 of "*Hi.*" *malpassii* to perform stable isotopic analyses on the carbon and oxygen. The results indicated that the $\delta^{13}C$ values for their Baccinello V3 samples fell between –13.2‰ and –12.6‰, and $\delta^{18}O$ values ranged from –3.6‰ to –3.1‰, for an intra-tooth range of 0.5‰, which suggests either a less seasonal rainfall and temperature regime, or more permanent, buffered water sources. They

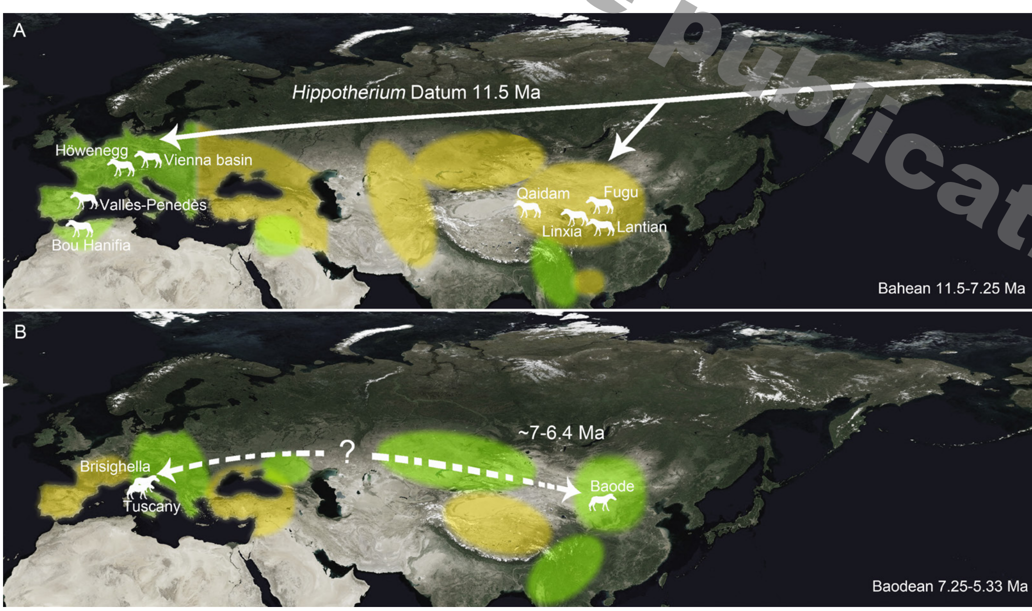

Fig. 4 Paleozoogeographical comparison of hipparion taxa in Bahean (A) and Baodean (B)
Dispersal routes are referred to Garcés et al. (1997) and present research
Greens and yellows distributed in Mid–latitude Asia, Europe and North Africa after Fortelius et al. (2014), respectively show the relatively close and open habitat

concluded that "*Hi.*" *malpassii* lived in a warm mesophytic subtropical woodland habitat. Kaakinen et al. (2013) suggested that many low-crowned species were found in Baode locality 49, from which "*Hi.*" *plocodus* was yielded. They mentioned five brachydont, C3-feeding taxa commonly seen at locality 49. The presence of these taxa indicated a closed habitat at this locality during the Late Miocene. Northern China became more humid during this time, as Kaakinen et al. (2013) pointed out, with the intensification of the East Asian summer monsoon or a weakening of the winter monsoon being the mechanism for this environment setting. Fortelius et al. (2014) estimated precipitation values during the Early Miocene to the Early Pleistocene (their Late Pliocene), and found that the average precipitation was higher in their "late Late Miocene (MN12–MN13, 8–5 Ma)" than that in their "early Late Miocene (MN9–MN11, 11–8 Ma)". In a recent paleoenvironmental investigation, Wang et al. (2021) performed multiple biomarker analyses, the results of which indicated that the Asian summer monsoon began to strengthen at around 6.5 to 5.6 Ma, and later showed substantially enhanced strength between 5.6 and 4.3 Ma. In the precipitation estimates of Fortelius et al. (2014), the environment in Europe was consistent in having a more humid situation than that of Asia from MN9 to MN13. During the Late Miocene, Europe had relatively closed habitats. During the Baodean, the development of the Asian summer monsoon restrained the aridification of North China and promoted the expansion of forests or woods. Some closed-habitat lineage originated in Eurasia and attempted to immigrate. During the late stages of the Late Miocene, the environment in North China was relatively humid and a significant expansion of the closed habitat took place. This closed-accepted lineage from Eurasia dispersed, via a route closed habitat was dominant, into North China where the environment was comfortable, giving rise to the species "*Hi.*" *plocodus* and the species "*Hi.*" *malpassii* which had a limited distribution in northern Italy, while the occurrences of *Hi. brachypus* in Europe and *Sh. dermatorhinum* in Asia likely represented another dispersion event (Fig. 4B).

6 Conclusions

(1) The controversial species *Hipparion plocodus* has been verified as a valid species ("*Hi.*" *plocodus*) based on the specialized morphological characteristics. A European species, which was previously identified as *Hippotherium malpassii*, has also been attributed as the closest group ("*Hi.*" *malpassii*) to "*Hi.*" *plocodus*.

(2) The phylogenetic analysis shows all the known species of Eurasian genus "*Hippotherium*" constitute a paraphyletic group, and "*Hi.*" *malpassii* was on a relatively derived position within the Eurasian species of hipparion horse, which has showed the clearly distant relation between "*Hi.*" *malpassii* and "*Hippotherium*". This result has also indicated that the record of stratigraphic range of "*Hippotherium*" after 7.25 Ma is absent

currently.

(3) The morphological and chronological comparisons suggest that "*Hi.*" *plocodus* and "*Hi.*" *malpassii* were two independent clades from one origin. The occurrence of "*Hi.*" *plocodus* in China represented a significant dispersal of hipparion horse from Europe into Asia, which was a response to global change of climate.

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旧大陆"*Hippotherium*"的存续：两种欧亚大陆三趾马的修订

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摘要：对一个具有争议的类群*Hipparion plocodus*进行了回顾。山西保德的头骨材料具有明确的鉴定特征，证实*Hi. plocodus*为一有效种。使用新的特征矩阵进行系统发育分析，表明*Hi. plocodus*和欧洲种*Hippotherium malpassii*构成一个单系群。事实上所谓的*Hm. malpassii*和*Hippotherium*属无较近的亲缘关系，而该属目前无晚中新世晚期分布记录。因此之前所定义的*Hi. plocodus*和*Hm. malpassii*在更好的材料发现之前暂时归入"*Hipparion*" 属当中。二者演化水平略有差异，时代相当，表明它们独立起源于某一更原始类群。在晚中新世晚

期，亚洲夏季风的盛行加强了中国地区的湿润程度，森林和灌木林生境在这一背景下迅速扩张。最终令欧亚大陆某一喜好封闭环境的类群向中国扩散，在这片适应的土地上演化出了“*Hi.*” *plocodus*。

关键词：系统分类修订，系统发育，欧亚三趾马，古动物地理

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